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Effects of native and nonnative arbuscular mycorrhizal fungi on growth and nutrient uptake of 'Pinot noir' (*Vitis vinifera* L.) in two soils with contrasting levels of phosphorus☆

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ABSTRACT

The influence of arbuscular mycorrhizal fungi (AMF) on growth and nutrient uptake by 'Pinot noir' grapevine cuttings was studied in an alluvial valley soil (Chehalis series, Mollisol) and a red-hill soil (Jory series, Ultisol) to better understand the role AMF play in vineyards planted in different soils with contrasting levels of available P. The first experiment compared plant response in both soils to a mix of AMF species (*Glomus mosseae*, *Glomus intraradices*, and *Scutellospora calospora*) isolated from Jory soil. Results showed that vine growth was heavily dependent on AMF in Jory soil, but inoculated and non-inoculated vines grew equally well in Chehalis soil. The increase in plant dry mass (274%) of 'Pinot noir' grown with AMF in Jory soil was primarily due to enhanced P uptake (833% increase). Uptake of most other nutrients was also enhanced by AMF in Jory soil. Sulfur was the only nutrient taken up in greater quantity by AMF vines in Chehalis soil. Root colonization by AMF was lower in Chehalis soil compared to Jory soil. A second experiment compared plant response in both soils to either native or nonnative *G. mosseae* isolated from each respective soil type. Vine growth in Chehalis soil was not affected by either *G. mosseae* isolate, although both isolates increased P and Zn uptake and the native isolate enhanced Cu and S uptake by 'Pinot noir'. Both *G. mosseae* isolates enhanced vine growth in Jory soil, primarily due to improved P uptake; however, the nonnative isolate of *G. mosseae* colonized roots to a greater degree and was more effective in promoting growth and nutrient uptake than the native isolate. Results from these experiments show that 'Pinot noir' is dependent on AMF to obtain enough P for normal growth in red-hill soils, while growth in valley soils is not dependent on AMF, even though P uptake can be improved by AMF in this soil. Native or nonnative *G. mosseae* isolates performed equally well in promoting P uptake in Chehalis soil, however, the Chehalis soil fungus outperformed the Jory soil fungus in promoting P uptake in Jory soil and Cu and S uptake in both soils.

1. Introduction

Grapevines (*Vitis* spp.) form mycorrhizal associations in fine roots with arbuscular mycorrhizal fungi (AMF) from the order *Glomales*. Numerous studies have shown that grapevines are dependent on AMF for normal growth and development (Menge et al., 1983; Linderman and Davis, 2001). AMF have been shown to increase P uptake by grapevines (Schubert and

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Cammarata, 1986; Giovannetti et al., 1988; Karagiannidis et al., 1995; Motosugi et al., 2002), but less is known about the role AMF play in the uptake of other plant nutrients by grapevines. AMF have been reported to increase N, K, Ca, Zn or Cu uptake in some studies (Biricolti et al., 1997; Petgen et al., 1998; Nikolaou et al., 2002), but it is unclear how universal these findings may be or whether uptake of these nutrients was due to improved P nutrition.

The red-hill soils (Ultisols of Jory, Bellpine, and Nekia series), which are highly weathered, acid soils of low fertility, are the most common vineyard soils found in the Willamette Valley region of Oregon (Brown, 1992). Extractable P concentrations (soil test values) in these soils are very low, often below 10 mg kg^{-1} (Schreiner and Linderman, 2005). Some vineyards have been planted on more fertile alluvial soils (Mollisols and Alfisols) located on the valley floor and lower hillsides in Oregon. A recent survey of Oregon vineyards showed that vines grown on either valley or red-hill soils had intense levels of root colonization by AMF, even though the valley soils were generally more fertile (particularly for P and Ca) than the red-hill soils (Schreiner and Linderman, 2005).

AMF that are native to a particular soil or site are often reported to be more effective mutualist's than nonnative fungi, presumably as a result of adaptation to edaphic factors such as soil nutrient concentrations, or to environmental factors such as drought (Lambert et al., 1980; Henkel et al., 1989; Boerner, 1990; Caravaca et al., 2003; Oliveira et al., 2005; Querejeta et al., 2006). However, in most studies native and nonnative AMF have not been compared in a uniform manner. The inoculum potential of different fungi has often not been equal leading to different levels of root colonization by different fungi, while in some cases a single nonnative species of AMF was compared to mixtures of native species. In addition, there are numerous reports where nonnative fungi have outperformed native fungi (Calvente et al., 2004; Trent et al., 1993; Sylvia and Burks, 1988). Whether native AMF are more effective symbionts than nonnative AMF in a particular soil remains unclear, especially if the host plant itself is not native to the site.

The purpose of this study was to understand whether grapevines grown in a red-hill soil (Jory series) would be more dependent on AMF to obtain nutrients (particularly P) and achieve adequate growth than vines grown in a higher fertility valley soil (Chehalis series). Based on our initial results, we tested the hypothesis that plant response and/or root colonization would be greater when plants were colonized by a fungus native to the experimental soil, as compared to the same species isolated from another soil. This was accomplished by comparing *Glomus mosseae* isolates obtained from each soil type, since this fungus was commonly isolated from both soils.

2. Materials and methods

2.1. Plant and soils

Both experimental soils (silty clay loam) were collected from 0 to 30 cm depth. Jory soil (fine, mixed, active, mesic Xeric Palehumult) was collected at the Oregon State University, Woodhall Research Vineyard located near Alpine, OR, USA (44°20′N, 123°24′W). Chehalis soil (fine-silty, mixed, superactive, mesic Cumulic Ultic Haploxeroll) was collected at the Oregon State University, Vegetable Research Farm located near Corvallis, OR, USA (44°34′N, 123°14′W). Both soils were mixed with coarse sand (pre-stress sand mix, Morse Bros Inc., Corvallis, OR) at a ratio of 1:1 based on volume. Dolomite lime (50% $CaCO_3$, 40% $MgCO_3$) was added to the Jory soil mix at rate of 50 g kg^{-1} dry soil to raise soil pH to a similar value as the Chehalis soil. Soils were air-dried at ambient temperature and sterilized by heating at 150 °C for 48 h to kill the resident AMF. Prior work with the Jory soil showed that steam-pasteurizing (77 °C) this soil led to excessive Mn concentrations (Schreiner, unpublished data). Sterilized soils were stored dry for 2–4 months prior to use. The properties of each soil (shown in Table 1) were determined from four random subsamples of each soil mix according to standard methods used for western Oregon soils as described in Schreiner (2005). Chehalis soil had higher levels of soil test P, K, Ca, and Cu than the Jory soil, and Jory soil had higher levels of S and organic matter. Chehalis and Jory soils will be annotated as CH and JY soils, respectively.

Pruning wood (1-year-old canes) of *Vitis vinifera* L. cv. 'Pinot noir' (FPS 91, Pommard clone) was collected in early February from the Woodhall Research Vineyard. Wood was stored moist at 4 °C for 3 months prior to producing three-bud cuttings used in our experiments. In experiment 1, three cuttings (plants) were stuck directly into the potted soils and allowed to root *in situ*. Two of the cuttings were removed from each pot (based on uniformity) after 5 weeks. In experiment 2, cuttings were pre-rooted in vermiculite:perlite (1:1) in a warm, mist chamber greenhouse for 4 weeks prior to transplanting a single plant in the potted soils. In both experiments, plants were grown in 4 L pots retaining a single shoot trained upright on a bamboo stake.

2.2. Experiment 1: test of mixed AMF in 2 soils

Experiment 1 was a 2 × 2 factorial design, with soil type and AMF as treatments. Six replications were included in each treatment for a total of 24 experimental units (potted plants). Within each soil type (CH and JY), half of the pots received a

Table 1 – Soil characteristics of Chehalis (Mollisol) and Jory (Ultisol) soils mixed 1:1 with sand (n = 4)

Soil	pH	NH_4-N	NO_3-N	P[a]	K	Ca	Mg	SO_4-S	Fe	Mn	B	Zn	Cu	%OM
Chehalis	5.8	22	4.9	59a[b]	172a	1647a	321	31b	78	72	0.19	1.6	1.7a	3.0b
Jory	5.9	28	5.5	24b	117b	1208b	299	101a	52	74	0.20	1.1	1.1b	4.7a

All nutrients expressed as mg kg^{-1} dry soil. Both soils were mixed with coarse sand and dry-sterilized (150 °C) prior to planting. Jory soil was amended with dolomite lime (50% $CaCO_3$, 40% $MgCO_3$) at 50 g kg dry $soil^{-1}$.

[a] Bray-1 method.

[b] Means followed by a different letter within a column are significantly different (Tukey's at 95% confidence level).

mixed inoculum of 3 AMF (+AMF) or not (control). AMF inoculum consisted of: *Scutellospora calospora* (Nicol. & Gerd.), Walker & Sanders INVAM# OR219, *G. mosseae* (Nicol. & Gerd.) Gerdemann & Trappe INVAM# OR218, and *Glomus* sp. INVAM#215, which had been previously isolated from JY soil from the Woodhall Research Vineyard. Each fungus was isolated and propagated by hand-picking spores from trap cultures and re-culturing with *Sorghum bicolor* L. in a low P, sandy loam soil. The +AMF treatments received 20 g of whole soil inoculum (containing spores, hyphae and colonized root fragments) from each fungal species. All pots received a microbial extract comprised of both experimental soils (untreated) and of the AMF inoculum to provide similar microflora organisms in the different treatments. This extract was prepared by wet-sieving equal proportions of live field soils (CH and JY) and AMF inocula soils (25 g each) through a 38 μm sieve three times.

Plants were grown in a greenhouse from 29 May to 27 September 2003 at Corvallis, OR, USA. Temperatures in the greenhouse were set at 15/25 °C, resulting in actual temperature ranges of 14–20/20–30 °C (night/day). Supplemental lighting was provided by 1000 W phosphor coated metal-halide lamps (General Electric, USA) on a 14 h photoperiod, providing ~500 μmol m^{-2} s^{-1} PAR at soil level. Plants were given water whenever the soil on the surface of individual pots became dry, and each plant was checked twice daily. On no occasion did plants show signs of water stress (wilted tips or leaves). Plants were fertilized with 400 mL of complete half-strength Hoagland's solution (Hoagland and Arnon, 1950) once every 2 weeks.

2.3. Experiment 2: test of native versus nonnative G. mosseae in two soils

Experiment 2 was a 2 × 3 factorial design, with soil type and AMF as treatments. Six replications were included in each treatment for a total of 36 experimental units (potted plants). Within each soil type (CH and JY), one-third of pots received inoculum of *G. mosseae* (INVAM #OR211a) isolated from the Chehalis soil (+CH G.m.), or inoculum of *G. mosseae* isolated from the Jory soil (+JY G.m.), or no AMF (control). The inoculum potential of each *G. mosseae* culture was determined by the MPN method using *S. bicolor* as host in 150 mL pots containing steam-sterilized, sandy loam soil (Daniels and Skipper, 1982). Each mycorrhizal pot received 300 infective propagules of the appropriate *G. mosseae* fungus. All pots received a microbial extract prepared as described for experiment 1.

Plants were grown in a greenhouse from 13 April to 12 July 2004 at Corvallis, OR, USA. Greenhouse temperatures, supplemental lighting, watering, and fertilization were as described for experiment 1. The main shoot of each plant was tipped at a height of 140 cm (when they reached the top of the bamboo stake) and subsequent shoot length measurements included lateral shoots that grew in response to tipping the main shoot. This was not necessary in experiment 1.

2.4. Measurements

Shoot lengths were measured periodically using a flexible tape ruler measuring from the base to the tip of each shoot, including lateral branches when present (experiment 2). At plant harvest, the dry mass of whole shoots (stems, leaves and petioles) was determined after oven drying at 70 °C for 7 days. Roots were gently washed free from soil and blotted dry. A 0.5–1.0 g random subsample of roots was removed and stored in 50% ethanol:5% acetic acid for the determination of root length and AMF colonization. Roots were cleared and stained with trypan blue according to Schreiner (2003). Root length was determined using the grid line intercept method (Newman, 1966) and AMF colonization was determined using the method of McGonigle et al. (1990) as modified by Schreiner (2003). The dry mass of remaining roots was determined as per shoots. All dried plant material was ground to pass through a 40 mesh (425 μm) screen to determine nutrient concentrations. N and S were determined by combustion analysis (CNS-2000 Macro Analyzer, Leco Inc., St. Louis, MO, USA) and P, K, Ca, Mg, Fe, Mn, B, Zn, and Cu were determined by ICP-OES (Optima 3000 DV, Perkin-Elmer Inc., Wellesley, MA, USA) after dry-ashing samples (Jones and Case, 1990).

2.5. Data analysis

Measured and calculated variables from both experiments were analyzed by ANOVA (soil type and AMF treatments as main effects). AMF colonization data were analyzed in the +AMF treatments only, resulting in a single factor ANOVA for experiment 1 (soil type) and a 2 × 2 ANOVA for experiment 2 (soil type and *G. mosseae* isolate as factors). Nutrient data from leaves, petioles, stems and roots were pooled to reduce the quantity of data shown. Whole plant nutrient contents for individual replicates were calculated from the concentration and dry mass data of the separated plant parts, and the whole plant nutrient concentrations were subsequently calculated from the sum of the contents divided by the total mass.

Planned comparisons of mean values were conducted to test for differences between noninoculated controls and +AMF vines within each soil type in both experiments, and to test for differences between the *G. mosseae* isolates in the second experiment. All statistics were carried out using Statistica software (version 6.1, Statsoft Inc., Tulsa, OK). The efficiency of nutrient uptake per unit root length was calculated by dividing the whole plant nutrient contents by the total root length of each plant. Data that violated assumptions of homogeneity of variance (Cochran's test) were log-transformed prior to analysis and the mean values presented in tables or figures represent back transformed means.

3. Results

3.1. Experiment 1: test of mixed AMF in two soils

Shoot growth of 'Pinot noir' was significantly greater in the CH control (no AMF) plants 57 DAP, as compared to all other treatments (Fig. 1). By 84 DAP, shoot length of the +AMF vines in CH soil was the same as the control treatment and remained the same thereafter. The +AMF vines in JY soil were significantly taller than controls in JY soil by 84 DAP and reached a similar height as the vines in CH soil by harvest.

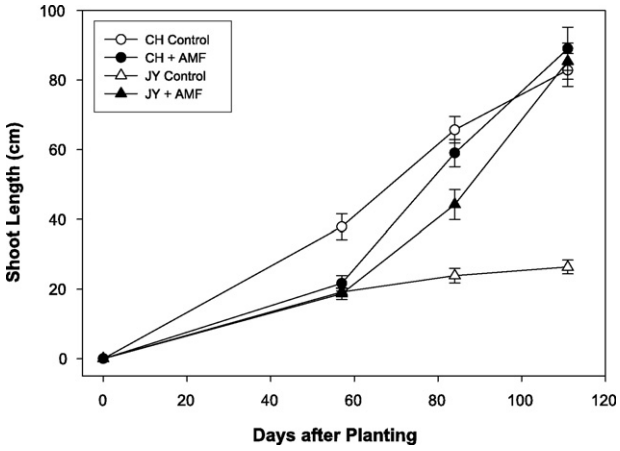

Fig. 1 – Shoot growth of 'Pinot noir' grapevines grown in Chehalis (CH) or Jory (JY) soils in the absence (control) or presence of the arbuscular mycorrhizal fungi *G. mosseae*, *G. intraradices*, and *S. calospora* (+AMF). Dormant cuttings were stuck directly into prepared soils. Data shown represent means (±standard errors) of six observations.

Control vines in JY soil reached a height of about 25% of the other treatments by the end of the experiment.

Shoot and root dry matter accumulation was significantly enhanced by AMF in JY soil, but not in CH soil (Table 2). Both shoots and roots of +AMF vines in JY soil had accumulated more than three times the mass of the control vines in JY soil. The shoot to root ratio was slightly greater in the JY versus CH soil, and in +AMF versus control treatments (main effects). AMF colonization of roots was greater in JY soil than CH soil for both the extent of root length colonized by any AMF structures (hyphae, arbuscules or vesicles) and the root length colonized specifically by arbuscules.

With the exception of Zn and Cu, nutrient concentrations in 'Pinot noir' vines were affected by soil type, AMF, or by an interaction between main effects (Table 3). A significant soil type by AMF interaction was found for N, P, K, Mg, Mn and B concentrations in vines. N and Mn responded similarly in that AMF increased their concentrations in CH soil, but reduced them in JY soil. Means comparisons showed that the influence of AMF on N and Mn concentrations was only significant in the JY soil. P and K responded similarly in that AMF increased their concentrations in both soils, but the effect was greater in the JY soil. AMF increased mean P and K concentrations in JY soil, but only K was significantly increased by AMF in the CH soil. Mg concentrations were unaltered by AMF in CH soil, and reduced by AMF in JY soil, while B concentrations were reduced by AMF in both soils with larger changes having occurred in JY soil. Ca and S concentrations were generally higher in vines grown in the JY soil, with S also at higher concentrations in +AMF vines (main effects). However, the mean S concentration of +AMF vines was significantly greater than the control vines only in CH soil. Plant Fe concentrations were higher in the CH soil compared to the JY soil (main effect).

The total content of most nutrients in 'Pinot noir' were significantly altered by an interaction between soil type and AMF (Table 3). P, K, Ca, Mg, Fe and B contents were all increased by AMF in JY soil, but not in CH soil, while S was increased in both soils with a greater increase in JY soil. Only N, Mn, Zn, and Cu contents showed no interaction between main effects. N, Mn, and Zn were increased by AMF in JY soil, with a similar but nonsignificant increase in CH soil. Cu was affected by AMF with generally higher content in +AMF vines, independent of soil type.

Phosphorus and K were the only nutrients that had both higher concentrations and contents in +AMF vines in JY soil, but the effect on P was much greater. Since plant mass was vastly increased by AMF in JY soil, growth was apparently limited by P in JY soil when AMF were absent. Increased contents of other nutrients in +AMF plants in JY soil were accompanied by either a reduction or no change in their concentration, indicating that greater uptake was due to improved growth of plants in response to improved P status. In the CH soil, where AMF had no impact on plant dry matter accumulation, S was the only nutrient taken up in greater quantity by AMF vines.

Table 2 – Plant growth and AMF colonization of 'Pinot noir' grapevines at Harvest (121 DAP) in experiment 1

Treatment	Biomass (g)		Shoot/root mass	Root length (m)	AMF colonization (% root length)	
	Shoot	Root			Total	Arbuscules
CH control	10.6	11.2	0.94	220	0[a]	0
CH + AMF	11.8	10.5	1.12	168	42.8	21.6
JY control	3.0	2.6	1.14	73	0	0
JY + AMF	11.8	9.3	1.29	178	67.4	39.9
(SE)	(0.8)	(0.4)	(0.07)	(15)	(3.3)	(1.6)
ANOVA effects (0.05)[b]	S, A, S × A	S, A, S × A	S, A	S, S × A	S	S
Contrasts[c]						
CH (Con vs. AMF)	ns	ns	ns	*	–	–
JY (Con vs. AMF)	***	***	ns	***	–	–

[a] Noninoculated controls were confirmed to be zero, but were excluded from analysis.
[b] Significant effects from ANOVA. S: soil type; A: AMF treatment; S × A: interaction between soil type and AMF treatment.
[c] (*) Significant <0.05; (**) significant <0.01; (***) significant <0.001; ns: not significant.

Table 3 – Whole plant nutrient concentrations and contents of 'Pinot noir' at Harvest (121 DAP) in experiment 1

Treatment	N	P	K	Ca	Mg	S	Fe	Mn	B	Zn	Cu
Concentration[a]											
CH control	6.9	1.25	9.6	11.3	3.81	0.68	409	125	17.1	13.1	3.09
CH + AMF	9.1	1.31	10.5	11.8	3.81	1.03	371	146	14.5	15.8	4.96
JY control	12.9	0.50	8.3	14.5	6.63	1.06	260	124	20.0	18.1	4.29
JY + AMF	10.0	1.16	10.5	13.3	5.20	1.22	241	93	13.9	11.4	4.49
(SE)	(0.7)	(0.04)	(0.3)	(0.6)	(0.17)	(0.08)	(34)	(9)	(0.5)	(3.2)	(0.78)
ANOVA effects (0.05)[b]	S, S × A	S, A, S × A	S, A, S × A	S	S, A, S × A	S, A	S	S, S × A	A, S × A	ns	ns
Contrasts[c]											
CH (Con vs. AMF)	ns	ns	*	ns	ns	*	ns	ns	**	ns	ns
JY (Con vs. AMF)	*	***	***	ns	***	ns	ns	*	***	ns	ns
Content[d]											
CH control	162	29.3	225	269	90	15.6	9.34	2.98	399	308	73
CH + AMF	219	31.4	251	281	91	24.7	8.83	3.46	345	379	123
JY control	65	2.5	42	74	33	5.3	1.34	0.63	101	92	22
JY + AMF	206	23.9	216	274	107	25.2	4.94	1.91	286	235	94
(SE)	(24)	(2.4)	(19)	(26)	(8)	(2.0)	(0.30)	(0.30)	(21)	(34)	(23)
ANOVA effects (0.05)[b]	S, A	S, A, S × A	S, A, S × A	S, A, S × A	S, A, S × A	S, A, S × A	S, A, S × A	S, A	S, A, S × A	S, A	A
Contrasts[c]											
CH (Con vs. AMF)	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns
JY (Con vs. AMF)	**	***	***	***	***	***	***	*	***	*	ns

[a] Concentrations of N, P, K, Ca, Mg and S reported as g kg^{-1}, and Fe, Mn, B, Zn and Cu reported as mg kg^{-1}.
[b] Significant effects from ANOVA. S: soil type; A: AMF treatment; S × A: interaction between soil type and AMF treatment; ns: not significant.
[c] (*) Significant <0.05; (**) significant <0.01; (***) significant <0.001; ns: not significant.
[d] Contents of N, P, K, Ca, Mg, S, Fe and Mn reported as mg $plant^{-1}$, and B, Zn and Cu reported as μg $plant^{-1}$.

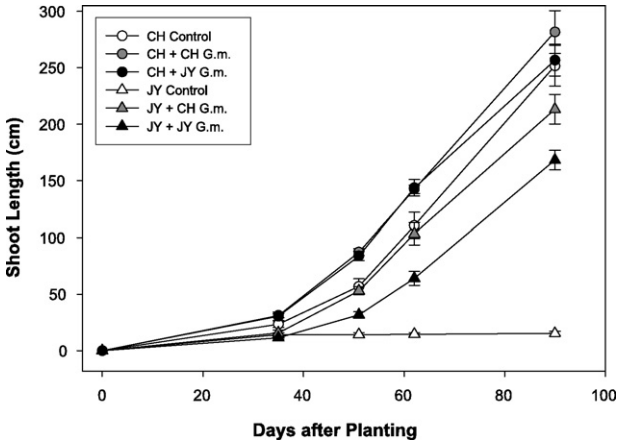

Fig. 2 – Shoot growth of 'Pinot noir' grapevines grown in Chehalis (CH) or Jory (JY) soils in the absence (control) or presence of the arbuscular mycorrhizal fungus *G. mosseae* isolated from Chehalis (+CH G.m.) or Jory (+JY G.m.) soils. Dormant cuttings were pre-rooted prior to planting into prepared soils. Data shown represent means (±standard errors) of six observations.

3.2. *Experiment 2: test of native versus nonnative G. mosseae in two soils*

The final shoot length of 'Pinot noir' was approximately three times greater in experiment 2 in all treatments except the JY soil control, as compared to experiment 1. The addition of either *G. mosseae* fungus to CH soil improved the growth of shoots slightly ($p < 0.05$) over the control treatment at 51 and 62 DAP, but controls were no different than the +AMF plants by 90 DAP (Fig. 2). Both *G. mosseae* isolates greatly enhanced shoot growth ($p < 0.001$) of vines in JY soil compared to the control, and the CH *G. mosseae* (nonnative fungus) had improved shoot growth better than the native fungus after 51 DAP. Control vines in JY soil only reached a height ~10% of the other treatments, and showed no increase after 35 DAP.

Dry matter accumulation was significantly enhanced by both *G. mosseae* isolates in JY soil, but not in CH soil (Table 4) similar to results from experiment 1. However, shoot mass in the CH soil was ~3 times greater in experiment 2 than in experiment 1. Root mass and root length were similar in both experiments in the CH soil. The shoot to root dry mass ratio of JY Control plants was similar to that found in experiment 1, with a value near 1, but this was increased to ~3 in all other treatments. Both *G. mosseae* isolates increased shoot dry mass in JY soil, but only CH *G. mosseae* significantly increased root dry mass in JY soil. AMF colonization of roots was similar in both fungal treatments in CH soil, but the CH *G. mosseae* (nonnative) had colonized roots to a greater degree than the JY *G. mosseae* (native) in JY soil. The frequency of root length with arbuscules was not significantly different between fungal isolates in the JY soil, but a trend of higher arbuscules by the nonnative *G. mosseae* was apparent.

Concentrations of all nutrients examined, except Fe, were affected by soil or AMF treatments or their interaction in experiment 2 (Table 5). A significant interaction between soil type and AMF treatments was found for K, Ca, Mg, Mn, B and Cu concentrations in vines. The concentration of K in plants was unaffected by AMF in CH soil, while it was improved by both fungal isolates in JY soil. The response of Ca, Mg, Mn, and B concentrations were similar in that these nutrients were unaffected by AMF in CH soil, but were reduced by AMF in JY soil. The interaction between soil type and AMF treatments for Cu was due to increased Cu concentrations in both soils when vines were colonized by the CH *G. mosseae* isolate, while Cu concentrations were unchanged (CH soil) or reduced (JY soil) in vines colonized by the JY isolate. Concentrations of N and S

Table 4 – Plant growth and AMF Colonization of 'Pinot noir' grapevines at Harvest (90 DAP) in experiment 2

Treatment	Biomass (g)		Shoot/root mass	Root length (m)	AMF colonization (% root length)	
	Shoot	Root			Total	Arbuscules
CH control	37.0	11.7	3.23	228	0[a]	0
CH + CH G.m.	35.9	13.5	2.71	251	76.5	29.4
CH + JY G.m.	39.5	12.3	3.44	235	68.1	27.6
JY control	2.0	1.8	1.14	58	0	0
JY + CH G.m.	24.8	8.3	3.15	175	80.3	36.1
JY + JY G.m.	18.0	5.0	3.71	124	59.4	26.6
(SE)	(2.6)	(1.2)	(0.21)	(18)	(3.1)	(3.4)
ANOVA effects (0.05)[b]	S, A, S × A	S,A	S, A, S × A	S, A, S × A	A	ns
Contrasts[c]						
CH (Con vs. CH G.m.)	ns	ns	ns	ns	–	–
CH (Con vs. JY G.m.)	ns	ns	ns	ns	–	–
CH (CH G.m. vs. JY G.m.)	ns	ns	*	ns	ns	ns
JY (Con vs. CH G.m.)	***	***	***	***	–	–
JY (Con vs. JY G.m.)	***	ns	***	*	–	–
JY (CH G.m. vs. JY G.m.)	ns	ns	ns	ns	***	*

[a] Noninoculated controls were confirmed to be zero, but were excluded from analysis.
[b] Significant effects from ANOVA. S: soil type; A: AMF treatment; S × A: interaction between soil type and AMF treatment; ns: not significant.
[c] (*) Significant <0.05; (**) significant <0.01; (***) significant <0.001; ns: not significant.

Table 5 – Whole plant nutrient concentrations and contents of 'Pinot noir' at Harvest (90 DAP) in experiment 2

Treatment	N	P	K	Ca	Mg	S	Fe	Mn	B	Zn	Cu
Concentration[a]											
CH Control	13.9	1.28	12.2	10.8	2.91	0.96	396	94	26.6	14.1	4.9
CH + CH G.m.	13.1	2.13	13.2	10.9	3.06	1.24	434	99	29.2	18.0	9.8
CH + JY G.m.	11.6	1.93	12.1	10.3	2.83	1.04	416	85	25.9	17.5	5.7
JY Control	19.6	0.67	9.0	16.2	5.02	1.50	555	154	59.6	15.0	10.3
JY + CH G.m.	15.5	1.84	12.7	11.7	3.83	1.55	305	85	28.8	15.7	12.3
JY + JY G.m.	17.2	1.23	12.6	11.9	3.73	1.27	278	70	23.9	13.9	5.3
(SE)	(1.1)	(0.11)	(0.7)	(0.5)	(0.14)	(0.08)	(69)	(8)	(2.3)	(0.9)	(0.7)
ANOVA effects (0.05)[b]	S	S, A	A, S × A	S, A, S × A	S, A, S × A	S, A	ns	A, S × A	S, A, S × A	S	S, A, S × A
Contrasts[c]											
CH (Con vs. CH G.m.)	ns	***	ns	ns	ns	*	ns	ns	ns	**	***
CH (Con vs. JY G.m.)	ns	***	ns	ns	ns	ns	ns	ns	ns	*	ns
CH (CH G.m. vs. JY G.m.)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	***
JY (Con vs. CH G.m.)	*	***	***	***	***	ns	*	***	***	ns	*
JY (Con vs. JY G.m.)	ns	**	***	***	***	*	**	***	***	ns	***
JY (CH G.m. vs. JY G.m.)	ns	***	ns	ns	ns	*	ns	ns	ns	ns	***
Content[d]											
CH Control	666	62	590	524	141	46.0	19.0	4.53	1.28	680	238
CH + CH G.m.	638	104	646	535	151	60.6	20.5	4.84	1.42	886	479
CH + JY G.m.	587	98	612	529	146	52.8	21.6	4.34	1.32	901	290
JY Control	73	2	34	60	19	5.6	2.0	0.57	0.22	56	38
JY + CH G.m.	460	56	394	369	122	47.4	10.0	2.51	0.86	498	380
JY + JY G.m.	380	27	282	268	84	28.6	6.5	1.58	0.53	309	117
(SE)	(23)	(4)	(31)	(31)	(10)	(2.7)	(2.7)	(0.23)	(0.06)	(56)	(24)
ANOVA effects (0.05)[b]	S, A, S × A	S, A, S × A	S, A, S × A	S, A, S × A	S, A, S × A	S, A, S × A	S	S, A, S × A	S, A, S × A	S, A, S × A	S, A
Contrasts[c]											
CH (Con vs. CH G.m.)	ns	***	ns	ns	ns	***	ns	ns	ns	*	***
CH (Con vs. JY G.m.)	*	***	ns	ns	ns	ns	ns	ns	ns	**	ns
CH (CH G.m. vs. JY G.m.)	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	***
JY (Con vs. CH G.m.)	***	***	***	***	***	***	ns	***	***	***	***
JY (Con vs. JY G.m.)	***	***	***	***	***	***	ns	**	***	**	*
JY (CH G.m. vs. JY G.m.)	*	***	*	*	*	***	ns	**	***	*	***

[a] Concentrations of N, P, K, Ca, Mg and S reported as g kg^{-1}, and Fe, Mn, B, Zn and Cu reported as mg kg^{-1}.
[b] Significant effects from ANOVA. S: soil type; A: AMF treatment; S × A: interaction between soil type and AMF treatment.
[c] (*) significant <0.05; (**) significant <0.01; (***) significant <0.001; ns: not significant.
[d] Contents of N, P, K, Ca, Mg, S, Fe, Mn, B and Zn reported as mg $plant^{-1}$, and Cu reported as μg $plant^{-1}$.

were generally higher in vines from JY soil, and P and Zn were generally at higher concentrations in vines from CH soil (main effects). P concentrations of vines were also generally higher in +AMF vines compared to controls, and higher in vines colonized by the CH *G. mosseae* isolate compared to the JY isolate independent of soil type (main effect). However, mean contrasts indicated that vines colonized by the CH isolate had higher P concentrations than vines colonized by the JY isolate in JY soil only.

Nutrient contents of vines from experiment 2 were largely affected by an interaction between soil type and AMF treatments (Table 5), similar to results from experiment 1. Only Fe and Cu were not affected by an interaction between main effects. Iron contents were generally higher in vines grown in CH soil compared to JY soil, and Fe contents were not altered by AMF. The content of Cu in vines was also higher in CH soil, but was increased in plants to a greater extent by the CH *G. mosseae* fungus than the JY fungus in both soils. The interaction between soil type and AMF treatments for K, Ca, Mg, Mn, and B was a result of higher contents of these nutrients in both +AMF treatments in JY soil (often with CH isolate greater than the JY isolate), with no effect of AMF in CH soil. Phosphorus and Zn contents of vines were increased by both fungi in both soils, but the CH isolate significantly improved P and Zn uptake better than the JY isolate in the JY soil. The content of N and S was increased by both isolates in JY soil (with the CH fungus outperforming the JY fungus in JY soil), but N content was unaffected by the CH fungus and reduced by the JY fungus in CH soil. Vine S content was increased by the CH fungus, but not the JY fungus in CH soil. In summary, the contents of most nutrients were higher in vines inoculated with either *G. mosseae* isolate in JY soil because of improved P uptake and growth, although the nonnative (CH) fungus outperformed the native (JY) fungus. A difference in P uptake between isolates was not apparent in CH soil.

The different *G. mosseae* isolates were further compared by analyzing the efficiency of nutrient uptake by roots (whole plant uptake per unit root length) in the different treatments (Fig. 3). Results showed that both *G. mosseae* isolates increased the efficiency of P uptake to a similar extent in CH soil, while the CH isolate increased P uptake efficiency to a greater extent than the JY isolate in JY soil (Fig. 3A). The efficiency of Cu uptake was improved by the CH *G. mosseae* isolate, but not by the JY isolate in both soils (Fig. 3B). The remaining macroelements (K, Ca, Mg, and S) as well as Mn, B, and Zn responded in a similar fashion as found for N, such that efficiency of uptake was not increased by either fungus in CH soil, but was increased by both fungi to a similar extent in JY soil (Fig. 3C). Neither fungus affected Fe uptake per unit root length in either soil type.

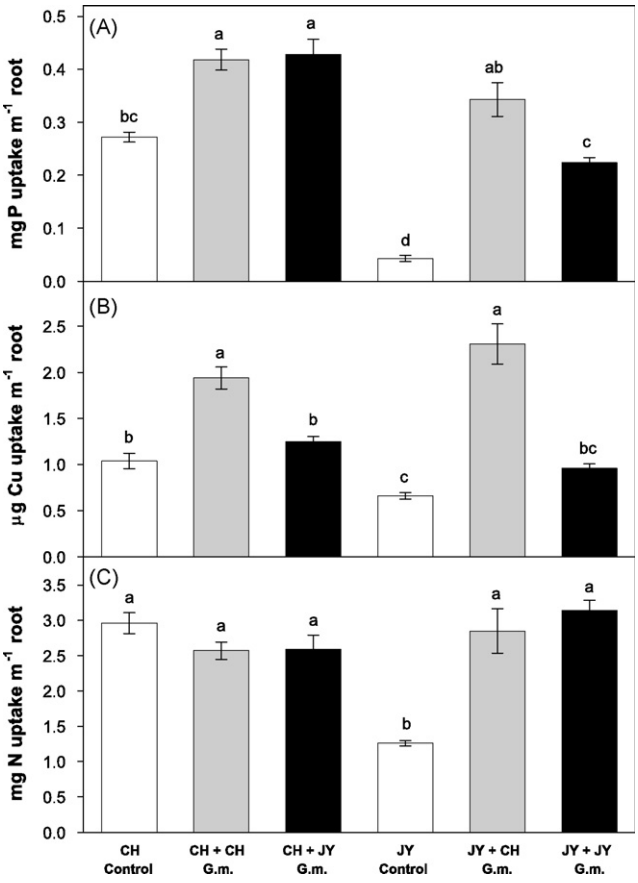

Fig. 3 – Efficiency of phosphorus (A), copper (B), and nitrogen (C) uptake by 'Pinot noir' grapevines grown in Chehalis (CH) or Jory (JY) soils in the absence (control) or presence of the arbuscular mycorrhizal fungus *G. mosseae* isolated from Chehalis (+CH G.m.) or Jory (+JY G.m.) soils. Data shown represent means (±standard errors) of six observations. Letters designate significant groups at 95% confidence (Tukey's).

4. Discussion

Results from both experiments in this study showed that 'Pinot noir' grapevines are heavily dependent on AMF to achieve normal growth in the low P, JY soil. This was shown to be the result of improved P uptake by mycorrhizal vines. While the uptake of other nutrients was also increased by AMF in JY soil, P uptake was improved to the greatest degree and the relative increase in P contents of vines was greater than the associated increase in plant dry mass in both experiments. Interestingly, the nonmycorrhizal (control) vines growing in JY soil did not display typical P deficiency symptoms (small dark green leaves with intervienal red regions) described for grapevines (Cook et al., 1983; Gärtel, 1996), but rather had small leaves with leaf margins often rolled upward. The redhill soils common in western Oregon typically have lower soil test P levels than the JY soil used in this study (Schreiner and Linderman, 2005), indicating that grapevines grown on these hillside Ultisols are reliant on AMF to supply their P requirements. Our results with grapevines in JY soil are consistent with previous findings of a large growth dependence of sweetgum (*Liquidambar styraciflua* L.) on AMF in the same soil series (Davis et al., 1983).

The lack of a growth response to AMF by 'Pinot noir' in the more fertile CH soil suggests that vines grown on similar soils can obtain ample P without AMF. These results are similar to findings with citrus, where dependence on mycorrhizal fungi became insignificant when soil test P levels (Bray-1)

approached 50 mg kg^{-1} (Ojala et al., 1983). However, successful establishment of grapevines in high fertility field soils in California was found to be dependent on AMF colonization of roots (Menge et al., 1983). Additional stress encountered under field conditions, which likely includes some degree of water stress, may therefore result in a greater dependence of field-grown grapevines on AMF than what is measured under more luxurious greenhouse conditions, like this study. Since soil P availability is reduced by soil water deficits even in high P soils (Gahoonia et al., 1994), it is possible that grapevines grown in CH soil would be dependent on AMF under drier soil conditions than tested here. The striking ability of AMF to improve P uptake by *Sorghum* under dry soil conditions shows that AMF may play a more important role in plant production in high P soils than previously thought (Neumann and George, 2004).

AMF significantly enhanced P uptake by 'Pinot noir' in CH soil only in experiment 2 in this study, when shoot growth of vines (and hence P demand) was much greater. These results are similar to prior work in this soil with peas, where the addition of AMF resulted in higher seed yield with no effect on vegetative growth (Schreiner and Bethlenfalvay, 1996). Additional access to P by mycorrhizal vines, even though P may be sufficient for vegetative growth, could potentially affect reproductive characters in the following growing season. Skinner and Matthews (1989) showed that reproductive development (flower initiation and differentiation) of young 'Carignane' grapevines was more sensitive to low P supply than vegetative growth. Enhanced uptake and storage of P, beyond what is required for immediate vegetative growth (as observed in experiment 2) may be of particular importance for heavily pruned crops like grapes, since most of the new shoot growth is removed every year. New canopy growth of mature 'Pinot noir' vines grown in a low P vineyard in Oregon were heavily dependent on P reserves in roots, and this was more pronounced in a drier year (Schreiner et al., 2006).

The uptake of nearly all nutrients examined in the present study (in addition to P) was enhanced by AMF in JY soil. Since P uptake was more greatly affected by AMF, however, the increased uptake of other nutrients by mycorrhizal vines in JY soil can be attributed to the release of the P limitation on growth. AMF have been shown to improve the uptake of other important plant nutrients like N, either directly from soil (Johansen et al., 1994; Mader et al., 2000), or indirectly via hyphal connections with other plants (Cheng and Baumgartner, 2004). The improved uptake of N and other nutrients by mycorrhizal 'Pinot noir' in JY soil in this study cannot be separated from the primary effect of AMF on P uptake, which resulted in a large stimulation (~4- to 7-fold) of dry matter accumulation.

AMF did not stimulate growth of shoots or roots of 'Pinot noir' in either experiment in CH soil. Therefore, higher accumulation of S, Zn or Cu that had occurred in mycorrhizal vines in CH soil (increased S uptake by mix of AMF in experiment 1; increased S and Cu uptake by the CH isolate in experiment 2; increased Zn uptake by both isolates in experiment 2) suggests that uptake of these nutrients was enhanced by AMF independent of P-induced growth effects. Improved uptake of S in mycorrhizal plants is not uncommon (Vander Zaag et al., 1979; Clark et al., 1999), and transport of sulfate along AMF hyphae has been shown (Cooper and Tinker, 1978). Often, however, S concentrations are lower in mycorrhizal plants owing to a dilution effect when growth is increased in response to improved P uptake (Marschner, 1996; Smith and Read, 1997). The higher S concentrations and contents found in mycorrhizal vines in experiment 1 and in the vines colonized by the CH *G. mosseae* isolate in experiment 2 in CH soil is the first evidence to our knowledge that AMF enhance plant uptake of S when P is not limiting. Our results of enhanced Cu and Zn uptake support prior findings in grapevines by Petgen et al. (1998), who showed that AMF stimulated Zn and Cu uptake of SO-4 grapevine rootstocks. Copper and Zn are commonly thought to be the second most important nutrients, after P, that are increased by AM fungal colonization (Marschner, 1996; Smith and Read, 1997; Lee and George, 2005).

The clear differences that occurred in plant Cu uptake between the isolates in our second experiment shows that these two populations of *G. mosseae* are physiologically distinct. The consistent effect on plant Cu uptake by both isolates when P was either limiting plant growth (JY soil) or not (CH soil) is strong evidence for a divergence in metal uptake capacity between these populations of *G. mosseae*. Phenotypic differences among isolates of this fungal species have been observed previously in symbiosis with soybeans under conditions where inoculum potential of different isolates was controlled (Bethlenfalvay et al., 1989). It is unknown whether the difference in Cu uptake between the two isolates in this study was due to a difference in the ability of the fungi to translocate or transfer Cu to the host plant, or to a difference in how the fungi may have altered the availability of Cu in soil. The lack of correspondence between P and Cu uptake in the present study confirms earlier findings that improved uptake of these nutrients by AMF are not linked, indicating that AMF enhance uptake of P and Cu by different mechanisms (Li et al., 1991; Lee and George, 2005). Differences in the level of root colonization cannot explain the observed difference in Cu uptake between *G. mosseae* isolates in this study, since both fungi colonized roots to the same degree in CH soil. However, differences in the amount of external hyphae produced by these fungi, which was not determined, could account for the divergent Cu uptake response.

The comparison of *G. mosseae* isolates in experiment 2 was conducted to test the hypothesis that the higher level of root colonization by AMF observed in JY soil in the first experiment was because the fungi used were better adapted to their native soil (i.e. colonization was lower in CH soil because the fungi used were isolated from JY soil). This hypothesis is rejected based upon the results from experiment 2. Both *G. mosseae* isolates colonized roots to the same degree in CH soil, while the nonnative isolate colonized roots better than the native isolate in JY soil. In addition, colonization by either fungus was not significantly different between soil types in the second experiment. It seems unlikely that soil specific adaptation of the JY fungi used in experiment 1 could explain the lower colonization in CH soil.

Another possible explanation for the lower AMF colonization in CH soil in experiment 1 is that the higher P status of this soil and of the vines grown in it resulted in host regulation of colonization (Koide and Schreiner, 1992). However, down regulation of colonization based upon higher P status does not

sufficiently explain these findings in lieu of experiment 2, where colonization by either *G. mosseae* isolate was not reduced in CH soil. P concentrations in the nonmycorrhizal control plants were nearly identical in both experiments in CH soil. Based on these observations, the vines grown in experiment 2 would have been more likely to reduce colonization in response to higher P status, which was not observed.

The greater effectiveness of the CH *G. mosseae* isolate (nonnative) in JY soil as compared to the native fungus was related to greater colonization of 'Pinot noir' roots by the CH soil fungus in that soil. A similar but nonsignificant trend of higher colonization by the CH isolate in CH soil was also found. These observations suggest that the inoculum potential of the CH *G. mosseae* isolate was slightly greater than the JY isolate, but the difference was only detected in JY soil. This could be explained by the fact that initial root growth was probably inhibited in JY soil (being P limited), which reduced the number of encounters with AMF propagules thereby accentuating a small difference in inoculum potential between the fungi. This probably did not occur in CH soil because roots would have more quickly filled the pot maximizing chances of contacting infective AMF propagules. These results indicate that differences in the symbiotic effectiveness when comparing different species or isolates of AMF can still be attributed to different levels of root colonization even when the inoculum potential of the fungi being compared is equal. This raises the question; what is the appropriate method for comparing physiological effects of different AMF on a given plant or ecosystem?

In conclusion, results from this study indicate that: (1) grapevines grown in the low P, red-hill soils (Ultisols) are heavily dependent on AMF to supply P needed for growth and ultimately the acquisition of other nutrients, (2) grapevines grown in the more fertile valley soils are less dependent on AMF, yet can still benefit in terms of greater P uptake, depending on plant demand for P (i.e. growth rate), (3) native isolates of AMF are not necessarily better adapted to specific soils in promoting growth and nutrient uptake of grapevines, and (4) differences in the capacity to enhance plant Cu uptake occurs within different populations of the same AM fungus, which could be exploited in developing function-specific inocula for practical use. Future research to clarify the impact of AMF on P nutrition of grapevines grown in higher fertility soils under drier soil conditions is warranted.

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